Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana

PETER LESICA
Conservation Biology Research, 835 Eighth Ave., Helena, MT 59601, U.S.A.
BRUCE MCCUNE[1]
Department of General Science, 355 Weniger Hall, Oregon State University, Corvallis, OR 97331-6505, U.S.A.
STEPHEN V. COOPER
Conservation Biology Research, 835 Eighth Ave., Helena, MT 59601, U.S.A.
AND
WON SHIC HONG
College of Great Falls, Great Falls, MT 59405, U.S.A.

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Lichen and bryophyte communities differed between managed second-growth and unmanaged old-growth grand fir forests in northwestern Montana in all three strata examined: lower canopy, trunk, and ground. Old-growth forests had larger trees, greater structural diversity, greater volumes of coarse woody debris, fewer species of vascular plants, more species of trunk epiphytes, higher β diversity, and higher γ diversity than second-growth forests. Although pendent fruticose lichens were common in both stand age classes, species of *Alectoria* were more abundant in old growth, while second growth was dominated by *Bryoria* spp. Nitrogen-fixing foliose lichens were more common in all strata of old growth, and *Lobaria pulmonaria*, a common N-fixing species in old growth, was absent in second growth. *Cladonia* spp. were more numerous in second-growth forests. Nearly all species of leafy liverworts were more common in old growth and typically occurred on rotting wood. Many of these liverworts were absent from second growth. Our results suggest that many species of lichens and bryophytes find optimum habitat in old-growth forests and that these species will become less common as silvicultural practices continue to convert old growth to younger aged forests.

Key words : bryophytes, diversity, forests, lichens, Montana, old growth.

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Les communautés de lichens et de bryophytes diffèrent entre les forêts de croissance secondaire aménagées et les vieilles forêts d'*Abies grandis* du nord-ouest du Montana, et ceci au niveau des trois strates examinées. Les vieilles forêts comportent de gros arbres, possèdent une diversité structurelle plus grande, montrent de plus forts volumes de gros débris ligneux, moins d'espèces de plantes vasculaires, plus d'espèces épiphytes sur les troncs, une plus forte diversité β et une diversité γ plus élevée que les forêts secondaires. Bien que les lichens fructiculeux décombants soient communs dans les stations des deux classes d'âge, les espèces d'*Alectoria* sont plus abondantes dans les vieilles forêts, alors que les forêts de seconde venue sont dominées par les *Bryoria* spp. Les lichens foliosés fixateurs d'azote sont plus fréquents dans toutes les strates de la forêt surannée, et le *Lobaria pulmonaria*, une espèce commune, fixatrice d'azote et typique des forêts surannées, est absente des forêts de seconde venue. Les *Cladonia* spp. sont plus communs dans ces forêts de seconde venue. Presque toutes les espèces d'hépatiques feuillées sont plus communes dans les forêts agées et se retrouvent typiquement sur du bois pourrissant. Plusieurs de ces hépatiques sont absentes des forêts de seconde venue. Les résultats suggèrent que plusieurs espèces de lichens et d'hépatiques trouvent leur habitat optimum dans les forêts surannées et que ces espèces deviennent moins fréquentes lorsque les pratiques sylvicoles continuent à convertir les vieilles forêts en forêts plus jeunes.

Mots clés : bryophytes, diversité, forêts, lichens, Montana, forêt surannée.

[Traduit par la rédaction]

Introduction

Logging has altered the presettlement stand age mosaic by systematically converting old growth to second growth. As a result, some species have become more common, while others have decreased. Although many species can occur in stands of all ages, others are more restricted. In the forests of Oregon and Washington, a number of plants and animals are dependent on old growth and many others find optimum habitat there (Thomas 1979; Franklin *et al.* 1981; Harris 1984; Norse 1989).

The importance of maintaining biological diversity on forest lands is now appreciated by both land management agencies and the public (Norse *et al.* 1986). An important problem in managing forests to protect biological diversity is understanding the extent and nature of dependence of all component strata and species on old-growth forests. The purpose of our study was to determine how the lichen and bryophyte components differ between old-growth grand fir forests and managed second-growth, rotation-age forests in the Swan Valley of northwestern Montana. By learning how silvicultural practices alter the dynamics of lichen and bryophyte communities, scientists and resource planners can better predict the effects of forest practices on these poorly understood organisms and on the other organisms that depend on them.

Relatively little is known about changes in the composition of lower plant communities through succession (Franklin *et al.*

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[1] Author to whom all correspondence should be addressed.

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1981). Trunk and ground layer lichen and bryophyte communities change with stand age in western Montana (McCune and Antos 1982). Changes in light penetration, wetting and drying cycles, and host tree bark characteristics appear to be important factors contributing to successional changes in mesic conifer forests (McCune and Antos 1981*a*, 1982). Differences in colonizing abilities among species may also account for changes through time (McCune and Antos 1981*b*). The present work extends those studies by contrasting managed second-growth stands near harvest and old-growth stands and by including branch epiphytes in the sampling.

Our initial study had two goals: to compare several methods for efficient sampling of each stratum (to be reported elsewhere) and to compare the lower-plant vegetation in old growth and second growth (reported here), employing methods we found most efficient.

Study area

We studied forests around the south end of Swan Lake at the north end of the Swan Valley, Lake County, Montana (Fig. 1). The Swan Valley is a straight, glaciated trough between the Mission and Swan ranges that crest about 1000 m above the gently undulating valley floor. The climate is strongly influenced by moist Pacific air masses. On average, the northern valley floor receives ca. 75 cm of precipitation annually. The winter months and June are relatively wet, while July and August are the driest months. Snowpack is usually over 1 m deep. Mean January and July temperatures are −5 and 17°C, respectively. The Swan Valley is predominantly forested, grand fir (*Abies grandis*) being the most abundant tree in mature forests on modal upland sites. On drier sites Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are prominent, while moist sites frequently support western red cedar (*Thuja plicata*). Western white pine (*Pinus monticola*) is a frequent component of moist forests, but is seldom dominant, and then only in old-growth stands. Antos and Habeck (1981) concluded that site moisture is the primary physical factor controlling community composition within the tolerance range of *A. grandis* in the Swan Valley.

In the winters of 1913 to 1917, 1200 ha of forest near the town of Swan Lake were clear-cut (Fig. 1). The logs were skidded out by horse during the winter. Logs were then transported by small gauge railroad to Swan Lake. In 1919 a large fire swept through much of the cutover area, burning the slash. These disturbances were similar to the modern-day silvicultural treatment of clearcut followed by broadcast burn of slash. However, the absence of dozer scarification and slash piling made this early clearcut less disruptive than many recent clearcuts.

Replacement stands were approximately 70 years old when we sampled them. Many of our stands were thinned during the 1960s, but records of this treatment no longer exist. Although much of the timber around this first clearcut has been harvested, a few stands of old-growth, virgin timber still exist in the lower foothills and outer edges of the valley floor. The oldest trees in these stands are typically just over 300 years old.

Methods

Field methods

We selected five second-growth and five old-growth stands on the valley floor or in the lower foothills (Fig. 1), all in the *Abies grandis*/*Clintonia uniflora* habitat type of Pfister *et al.* (1977). By sampling stands in a single habitat type we limited our study to sites that were relatively homogeneous in terms of soils, topography, and climate. Stands represented the range of old-growth and 1914 clearcut second-growth forests in this habitat type in the study area.

The two southern blocks of 1913–1917 clearcut (Fig. 1) were colder sites, as indicated by the prominence of *Abies lasiocarpa* and other species. Therefore, these blocks were excluded from sampling. Although this reduced the sample of second growth to a single clearcut block, the block is so large that it must have spanned many stands of different histories and site conditions.

Selection of old-growth stands was greatly constrained by their availability. We found only five stands of old-growth in the study area that met our criteria as stated above.

Focusing on a particular disturbance reduced the heterogeneity of our sample of second-growth stands, because the peculiarities of conditions during stand initiation appear to affect the long-term development of forests (McCune and Allen 1985). While studying a particular disturbance heightened the contrast between old growth and that class of second-growth stands, it reduced the scope of our conclusions. For example, it is likely that second-growth stands arising after wildfire are quite different from these former clearcuts.

Stands were sampled on August 18–27, 1989, alternating between old growth and second growth on consecutive days. Within a 0.081-ha circular plot, we measured diameter at breast height (dbh) of all trees over 13 cm dbh. We measured heights of ca. 10 trees using a tape and clinometer and then estimated the height of all remaining trees in the plot. Representative trees in each major size class were aged by counting annual growth rings on breast-height increment cores, then adding 7 years to compensate for time to reach breast height.

In each plot we established a 32-m reference line through the plot center and three sampling lines, 30 m long, perpendicular to the reference line. The middle sampling line ran through plot center, while the other two crossed the reference line 8 m on either side of plot center. We dug a small pit and measured the depth of litter and duff at three equidistant points along each sampling line, for a total of nine pits per plot. We measured the diameter of all down logs intercepted by half of each sampling line (45 m cumulative distance). Only logs greater than 8-cm diameter with more than half the diameter above ground level were recorded. This is a more conservative approach than used by researchers on the Pacific slope (Spies *et al.* 1988) and probably underestimates the amount of rotten logs. We classified each down log as either sound or rotten using a modification of a system developed for Pacific slope Douglas-fir forests (Sollins 1982). Each log was scored from 1 to 5 for structural integrity of both the bole and the branch system. The sum of these two scores determined whether the log was classified as sound (sum = 2–6) or rotten (sum = 7–10). Volumes of down logs were based on formulas of Howard and Ward (1972).

In each of three strata (described below), cover classes were assigned to macrolichen species (excluding crustose lichens), mosses, and liverworts in subplots (microplots or belt transects). Cover classes were 0–1%, 1–5%, then 10% increments to 95%, then 95–100%. Cover of each vascular plant species was also scored using these cover classes.

We sampled lichens and bryophytes in three strata: lower canopy, trunk, and ground. To estimate the abundance of macrolichens and bryophytes in the lower canopy stratum (trees and tall shrubs), we used a pole pruner to collect the branch closest to each sampling line at eight equidistant points along each line, for a total of 24 branches per plot. Branches, both living and dead, were collected from heights of 2–8 m above the ground. Branches shorter than 1 m were excluded. Using a metre stick placed along the middle 1-m section of the branch, we estimated cover of each species on the upper half-cylinder of the branch. Each 1-m branch segment was considered a microplot. Such cover class data are generally related to epiphyte biomass, even for species with three-dimensional growth forms (McCune 1990).

In the trunk epiphyte stratum we estimated cover of macrolichens and bryophytes on trees and shrubs larger than 13 cm dbh in 0.5 × 0.2 m flexible quadrats, 1.5 m above the ground, one on the north side and one on the south side of each tree sampled. At 6, 12, 18, and 24 m along each sampling line, we sampled the stem closest to the line for a total of 12 trees and 24 microplots per plot.

The ground layer included bryophytes and lichens growing on the forest floor (soil, duff, litter, and woody debris). The occasional rock surfaces were not sampled to standardize our measurements to surfaces that could be found in all stands. Three belt transects were defined by the sampling lines. Each transect was 30 m long and 1 m wide on both sides of the sampling line for a total of 60 m^2/line and 180 m^2/plot.

In addition to the cover estimates, we searched each stratum for species not observed in quantitative samples. The quantitative sampling techniques used here were fairly efficient for estimating species richness and species abundance (McCune and Lesica 1991).

Nomenclature of lichens, mosses, liverworts, and vascular plants generally follows Egan (1987), Lawton (1971), Stotler and Crandall-Stotler (1977), and Hitchcock and Cronquist (1973), respectively. "*Bryoria fuscescens*" as used here includes the closely related species *Bryoria lanestris* and small amounts of *Bryoria glabra*. Voucher specimens for lichens and mosses are in McCune's herbarium while vouchers for liverworts are in Hong's herbarium.

Data analysis

α diversity was measured as species richness and with the Shannon Index (Magurran 1988). β diversity was computed as the total number of species found in all 10 plots divided by the average number found in a single plot (Whittaker 1972). γ diversity (op. cit.) was estimated as the total number of species found in all five plots within each stand age class.

Are species found in only one of the two stand age classes equally likely to be found in old growth and second growth? We answered this question for each stratum by reference to a cumulative binomial distribution. The resultant probabilities indicate the likelihood of the result by chance alone, assuming equal probabilities ($p = 0.5$) of occurrence in each of the two stand age classes.

Cover classes in microplots or belt transects were converted to percentage cover in a whole plot by first converting the cover classes to midpoints of the intervals, then averaging those values using program SUMMARY in PC-ORD (McCune 1987). Before statistical analysis, all variables were screened by calculating descriptive statistics. Variables were transformed according to the results of this screening. Variables or classes of variables with a strong positive skew (>1.5) were $\log_e$ transformed. All percent cover variables were converted to proportions of one, then arcsine – square root transformed to improve normality and homogeneity of variance in the two groups of data.

Means for all variables were compared between old-growth and second-growth stands with two-sample *t*-tests using SPSS/PC+ (SPSS 1988). Probabilities of type I errors were calculated using separate variance estimates for the two groups (by adjusting the degrees of freedom) rather than pooled variances. This is a more conservative approach (less likely to detect a difference) than the normal pooled variance estimate. This seemed appropriate, considering the departures from normality and inhomogeneity of variances across groups that are typical of quadrat data. Because of our small sample size, the *t*-tests have low power to detect a difference; only large differences will be found significant. Applying a strict p (type I error), say of 0.05, will result in a high p (type II error), and one would frequently accept the null hypothesis of no difference when the null hypothesis was false. Therefore we chose a level of $p = 0.10$ as our upper limit for statistical significance to reduce p (type II error).

The *t*-values measure the differential between old growth and second growth and indicate the degree of specificity that a species has for one of the two age classes. Negative *t*-statistics indicate more cover in old growth, while positive *t*-statistics indicate more cover in second growth.

Difference in community composition of old-growth and second-growth stands was tested with Multi-response Permutation Procedures (MRPP; Mielke 1984) using program MRPP in PC-ORD (McCune 1987). MRPP provides a nonparametric multivariate test of the hypothesis of no difference between two or more groups, based on a matrix of Euclidean distances. The test statistic describes the separation between groups in an n-dimensional space. Smaller or more negative values indicate more separation between groups. The probability value expresses the likelihood of finding a difference as extreme as or more extreme than the observed difference between groups, based on all possible partitions of the data set.

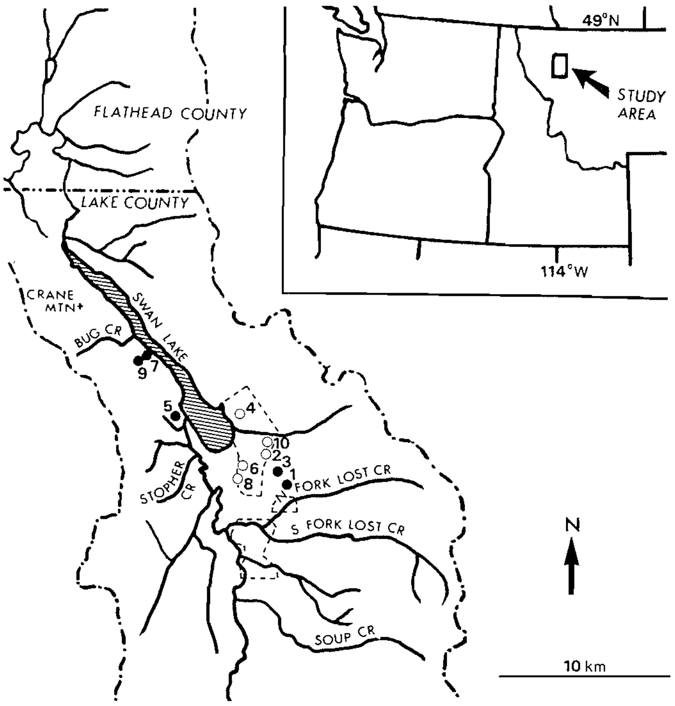

FIG. 1. Study area. Numbers show the locations of stands. ●, old-growth stands; ○, second-growth stands. The broken line shows the approximate boundaries of the 1913–1917 clearcuts.

Results

Site characteristics

Slope, elevation, and amount of exposed rock were similar for all plots and did not differ statistically between the old-growth and second-growth plots. All plot elevations were between 945 and 1100 m, and with the exception of one old-growth plot with a slope of 21%, all plots had a slope of less than 7%. All plots had less than 1% exposed rock. All old-growth stands were at least 13 ha, and plots were always at least 50 m from the nearest boundary with second growth. Because the sites were so similar, it is unlikely that the observed differences (below) between old-growth and second-growth stands could have been caused by a consistent difference in one or more site variables.

Vascular vegetation

Stands were dominated by grand fir, western white pine, western larch (*Larix occidentalis*), Douglas-fir, and lodgepole pine (*Pinus contorta*). The first two species had higher canopy cover in old growth, while the latter three were more abundant in second growth. Common shrubs included *Acer glabrum*, *Amelanchier alnifolia*, *Linnaea borealis*, *Spiraea betulifolia*, and *Vaccinium globulare*. Shrubs were notably more common in second growth. Common ground layer vascular plants included *Aralia nudicaulis*, *Clintonia uniflora*, *Pteridium aquilinum*, *Smilacina stellata*, *Viola orbiculata*, and *Xerophyllum tenax*. Vascular plant diversity was higher in second growth than in old growth (Table 1).

Mean age of dominant trees was 73 in second growth and 324 in old growth (Table 2). On average, old-growth forests

TABLE 1. Species richness, Shannon index, β diversity, and γ diversity for lichens, mosses, and liverworts in second-growth and old-growth stands in the Swan Valley

	Second growth	Old growth	t	p
Species richness				
Branch epiphytes	27.0 (1.8)	24.0 (3.1)	1.86	0.111
Trunk epiphytes	17.4 (1.6)	23.2 (3.1)	−3.67	0.011
Ground layer	24.0 (3.8)	29.8 (5.4)	−1.95	0.090
Vascular plants	44.8 (0.4)	38.6 (2.2)	5.24	0.005
Shannon index				
Branch epiphytes	2.38 (0.11)	2.31 (0.25)	0.45	0.667
Trunk epiphytes	2.27 (0.09)	2.11 (0.33)	0.93	0.400
Ground layer	2.95 (0.04)	3.12 (0.18)	−1.75	0.146
Vascular plants	2.85 (0.07)	2.49 (0.09)	5.95	0.001
β diversity[a]				
Branch epiphytes	1.22	1.38		
Trunk epiphytes	1.38	1.47		
Ground layer	1.67	1.91		
Vascular plants	1.52	1.40		
γ diversity[b]				
Branch epiphytes	33	33		
Trunk epiphytes	24	34		
Ground layer	40	57		
Vascular plants	68	54		

NOTE: Values are calculated using data from microplots for the canopy and trunk strata and belt transects for the ground stratum. Values of t and the associated probability are given where applicable. Standard deviations are given in parentheses.

[a] Total number species divided by mean number species per plot.

[b] Total number species in each age class.

had twice the basal area of second growth, while second growth had nearly three times the density of live trees as in old growth (Table 2). Old-growth stands had larger (greater diameter) and somewhat taller trees than second growth. The mean coefficient of variation (CV) of dbh was 31 and 57% for second growth and old growth, respectively ($p < 0.001$). The mean CV of height was 20 and 45% for second growth and old growth, respectively ($p < 0.001$). These statistics reflect the greater structural heterogeneity of the old-growth forests.

Dead material

Standing dead trees over 50 cm dbh averaged 15/ha in old-growth stands. There were no standing dead of this size in the second-growth plots (Table 2). Although mean density of standing dead trees was 32/ha and 69/ha for second growth and old growth, respectively, this difference was not significant ($p = 0.25$) owing to the large variation among stands (Table 2). Basal area of standing dead was lower in second growth than in old growth ($p = 0.02$, Table 2).

Depth of both litter and duff did not differ significantly between the two stand age classes (Table 2). The total volume of down logs was greater for old growth than second growth ($p = 0.04$, Table 2). Volumes of both sound and rotten down logs was also greater for old growth than second growth, but differences were only marginally significant because of large variances (Table 2). In second-growth stands that had been clear-cut, most down logs would be from the previous stand and thus for our study plots, at least 70 years old. The only recent input would be from self-thinning or precommercial thinning, and most of this would be small diameter. On the other hand, in the old growth, there has been an ongoing input of large diameter, down logs since before the last stand replacement event.

Lower plant communities

Lower plant communities differed between second growth and old growth for all three strata (MRPP; Table 3). These results are due to both differential presence of species and differences in the abundance of species. In the following sections, differences are examined by stratum: branch epiphytes, trunk epiphytes, and ground-layer cryptogams.

Branch epiphytes

A total of 45 species of macrolichens, 4 species of moss, and one liverwort were identified in the lower canopies of the 10 stands (Table 4). Seventeen species were found in only one stand age class, 12 of these in old growth and 8 in second growth (Table 4). Branch epiphyte species richness and the Shannon index differed little between second growth and old growth, while β (among stand) diversity was somewhat higher in old growth (Table 1).

Three species of lichens had more cover in old growth than in second growth, while eight species had higher cover in second growth ($p < 0.1$, Table 4). Of the four common, pendent, fruticose species, the two species of *Bryoria* had more cover in second growth ($p < 0.1$), while *Alectoria sarmentosa* had more cover in old growth ($p = 0.02$, Table 4). *Cetraria platyphylla* was more abundant in second growth, in old growth being mostly confined to treetop branches. *Lobaria pulmonaria*, a nitrogen-fixing foliose species, was relatively common in lower canopies of old growth but absent from second growth. *Platismatia glauca*, one of the most common lichens in moist western Montana forests, was sparse in second growth but was often luxuriant in old growth. Old-growth stands also contained species that are uncommon to rare in the northern Rockies including the moss *Antitrichia curtipendula* and the lichens *Ramalina thrausta* and *Nephroma helveticum*. *Ahtiana sphaerosporella*, which was more common in second growth, is uncommon at low elevations in western Montana, although it is common on *Pinus albicaulis* at high elevations.

Trunk epiphytes

A total of 50 species of macrolichens, 24 species of mosses, and 3 species of liverworts were identified from tree trunks in

TABLE 2. Live tree statistics, coarse wood debris, and depth of litter and duff for five second-growth and five old-growth stands in the grand fir habitat type in the Swan Valley

	Second growth	Old growth	t	p
Living tree statistics				
Mean age of dominant trees	73.3 (4.6)	323.8 (13.0)	−39.54	<0.001
Density (trees/ha)	1254.0 (1286.9)	472.0 (234.0)	1.44[a]	0.195
Mean density of trees > 50 cm dbh (trees/ha)	0 (0)	87.0 (31.1)		
Basal area (m^2/ha)	27.3 (2.9)	56.9 (13.2)	−4.66	0.005
Mean diameter of trees > 13 dbh (cm)	24.2 (2.9)	33.8 (4.3)	−4.12	0.004
Mean coefficient of variation for diameter (%)	31.2 (4.3)	57.4 (3.7)	−10.25	<0.001
Mean height of trees > 13 cm dbh (m)	20.9 (1.5)	23.4 (2.0)	−2.26	0.054
Mean coefficient of variation for height (%)	20.1 (5.2)	44.5 (3.7)	−8.57	<0.001
Coarse woody debris				
Density of standing dead >50 cm dbh (trees/ha)	0 (0)	14.8 (26.8)		
Density of standing dead (trees/ha)	32.1 (24.1)	69.2 (43.4)	−1.25[a]	0.252
Basal area of standing dead (dm^2/ha)	1.1 (1.6)	7.6 (7.2)	−2.90[a]	0.022
Volume of standing dead (m^3/ha)	8.4 (14.4)	77.2 (72.4)	−2.96[a]	0.021
Total volume of down logs (m^3/ha)	45.3 (58.2)	163.4 (83.7)	−2.71[a]	0.035
Volume of sound down logs (m^3/ha)	1.8 (2.8)	58.4 (66.9)	−1.98[a]	0.099
Volume of rotten down logs (m^3/ha)	43.5 (58.2)	105.0 (86.8)	−1.70[a]	0.134
Litter and duff				
Mean depth of litter (cm)	1.4 (0.4)	1.6 (0.4)	−0.65	0.532
Mean depth of duff (cm)	3.7 (1.1)	4.1 (0.9)	−0.59	0.572

NOTE: Standard deviations are given in parentheses.

[a] Values of t and p were obtained from log-transformed data for these variables, but means and standard deviations are from untransformed data.

the 10 stands (Table 4). Of the 38 species recorded in the microplots, 18 occurred in only one of the two stand age classes, and 14 of these only in old growth (Table 4), more than expected by chance alone ($p = 0.015$). These results suggest that more species of uncommon trunk epiphytes find suitable habitat in old-growth forests. Species richness, β diversity, and γ diversity were higher in old growth, while the Shannon index did not differ significantly (Table 1). Thus, both within-stand and among-stand species richness was higher in old growth.

Of the 20 species occurring in microplots in both old growth and second growth, two had higher cover in second growth and seven had higher cover in old growth ($p < 0.03$, Table 4). Of the three common species of pendent fruticose lichens, *Alectoria sarmentosa* and *Bryoria capillaris* were more common in old growth ($p < 0.03$), while *Bryoria fuscesens* was common in both stand age classes. All eight species of nitrogen-fixing foliose lichens encountered on trunks (*Leptogium saturninum, Lobaria pulmonaria, Nephroma* spp., and *Peltigera* spp.) were recorded only in old growth. Although most of these species were infrequent, *Lobaria* was fourth in abundance in the trunk stratum of old growth (Table 4). *Ptilidium pulcherrimum*, the only species of liverwort recorded in the trunk microplots, was found in all old growth plots but in no trunk microplots in second growth.

TABLE 3. Tests of differences in species composition between old-growth and second-growth stands, based on MRPP

	Avg. within-group distance			
	Second growth	Old growth	T	p
Branch epiphytes				
Ocular whole plot	3.18	2.67	−3.93	0.003
Microplots	0.21	0.19	−5.42	0.002
Trunk epiphytes				
Ocular whole plot	0.23	0.30	−5.36	0.002
Microplots	0.08	0.17	−5.48	0.002
Ground layer				
Ocular whole plot	0.21	0.24	−4.37	0.002
Belt transects	0.02	0.04	−2.23	0.028
Vascular plants				
Ocular whole plot	0.75	0.67	−5.05	0.001

NOTE: Euclidean distance was used as the measure of within-group distance.

Ground layer

Thirty-seven species of mosses, 23 species of lichens, and 11 species of liverworts were identified in the ground layer in the 10 stands (Table 5). Of the 64 species recorded in the belt transects, 29 occurred in only one stand age class, and 23 of these only in old growth (Table 5). Thus, uncommon ground layer mosses and liverworts were found in old growth more often than in second growth ($p = 0.003$). This difference was due mainly to mosses and liverworts (Table 5). Species richness, β diversity, and γ diversity were greater in old growth than second growth (Table 1), suggesting that both within-stand and among-stand diversity are greater in old growth. However, the difference in species richness was of marginal statistical significance ($p = 0.09$) because of the relatively large variance among plots.

Four species of nitrogen-fixing foliose lichens were recorded in the ground layer. Both species of *Nephroma* were found only in old growth, and both species of *Peltigera* were found in both second growth and old growth (Table 5). Although certainly not regionally restricted to old growth, two relatively common species of mosses, *Eurhynchium pulchellum* and *Heterocladium procurrens*, were found in our plots only in old growth. Two of the three most abundant liverworts, *Anastrophyllum hellerianum* and *Jamesoniella autumnalis*, were recorded only in old growth (Table 5). Of the 11 species of liverworts identified during our study, 7 were found only in old growth, and one, *Lophozia longiflora*, was found only in second growth (Table 5). More of these species were found in

TABLE 4. Frequency of occurrence (f = number of stands), mean percent cover ($\bar{x}$), and standard deviation of percent cover (s) for branch and trunk epiphytes in five second-growth and five old-growth stands

	Branch epiphytes								Trunk epiphytes							
	Second growth			Old growth					Second growth			Old growth				
	f	$\bar{x}$	s	f	$\bar{x}$	s	t	p	f	$\bar{x}$	s	f	$\bar{x}$	s	t	p
Lichens																
Ahtiana sphaerosporella	1	+	+	0	0	0										
Alectoria imshaugii	5	0.09	0.11	5	0.14	0.13	−0.83	0.430	4	0.09	0.07	5	0.53	0.38	−3.08	0.019
Alectoria sarmentosa	5	0.24	0.10	5	2.80	1.75	−3.54	0.022	5	0.13	0.08	5	0.99	0.35	−6.96	<0.001
Bryoria abbreviata	4	0.05	0.04	2	0.10	0.20	0.07	0.946	1	+	0.01	0	0	0		
Bryoria capillaris	5	1.35	0.86	5	3.12	1.78	−1.80	0.120	5	0.28	0.26	5	0.81	0.39	−2.73	0.026
Bryoria fremontii	4	0.14	0.22	1	0.03	0.08	1.31	0.231	2			2				
Bryoria fuscesens	5	2.23	0.82	5	0.31	0.16	6.33	0.001	5	0.67	0.32	5	0.50	0.27	0.96	0.364
Bryoria oregana	4	0.05	0.07	4	0.04	0.05	0.01	0.992	3	0.02	0.02	3	0.01	0.01	0.26	0.801
Bryoria pseudofuscesens	5	2.13	2.05	4	0.21	0.18	2.27	0.075	4	0.07	0.06	4	0.13	0.23	−0.29	0.783
Cetraria canadensis	4	0.06	0.08	0	0	0			3	0.02	0.02	0	0	0		
Cetraria chlorophylla	5	0.71	0.26	5	0.51	0.31	1.06	0.322	5	0.18	0.13	5	0.44	0.10	−3.34	0.015
Cetraria idahoensis	5	8.24	6.05	5	4.60	2.35	1.12	0.310	4	0.24	0.29	2	0.04	0.06	1.45	0.197
Cetraria merrillii	3	0.05	0.05	2	0.01	0.01	1.36	0.224	1	0.01	0.03	0	0	0		
Cetraria orbata	5	1.23	0.61	4	0.06	0.62	1.35	0.226	4	0.05	0.03	1	0.01	0.03	1.97	0.084
Cetraria pallidula	2			0												
Cetraria pinastri	1			0					4			1				
Cetraria platyphylla	5	2.01	0.96	3	0.06	0.06	7.55	<0.001								
Cladonia cenotea									0			5				
Cladonia chlorophaea									0	0	0	1	+	0.01		
Cladonia coniocraea									0	0	0	4	0.04	0.06		
Cladonia fimbriata	0			1					1	+	+	2	0.01	0.01	−0.81	0.446
Cladonia sulphurina									0			1				
Cladonia umbricola									0			1				
Fistulariella sp.	1			0					1			0				
Hypogymnia enteromorpha	3	0.20	0.26	3	0.77	1.36	−0.68	0.526	0	0	0	4	0.28	0.41		
Hypogymnia imshaugii	5	1.28	0.65	4	0.49	0.44	2.25	0.057	5	0.26	0.19	2	0.01	0.01	4.28	0.008
Hypogymnia metaphysodes	5	1.65	1.22	5	0.70	0.29	1.87	0.118	0	0	0	3	0.09	0.16		
Hypogymnia occidentalis	5	1.82	1.10	5	3.10	2.61	−0.80	0.452	4	0.16	0.13	5	0.07	0.05	0.91	0.389
Hypogymnia physodes	5	8.14	1.79	5	1.06	0.70	7.61	<0.001	4	0.21	0.29	5	0.46	0.28	−1.66	0.139
Hypogymnia rugosa									0	0	0	1	0.08	0.19		
Hypogymnia tubulosa	5	0.66	0.18	5	0.58	0.27	0.64	0.544	0	0	0	4	0.02	0.02		
Leptogium saturninum	0			1					0			1				
Letharia vulpina	3	0.02	0.02	0	0	0			0	0	0	2	0.01	0.01		
Lobaria pulmonaria	0	0	0	3	0.67	1.27			0	0	0	3	1.41	1.98		
Melanelia multispora	2	0.36	0.73	1	+	0.01	1.19	0.299	1			1				
Melanelia subaurifera	5	0.62	0.95	2	0.06	0.08	2.00	0.099	4	0.03	0.02	0	0	0		
Melanelia subelegantula	4	0.04	0.03	4	0.27	0.30	−1.55	0.184	2			2				
Nephroma helveticum	0	0	0	1	0.08	0.19			0			1				
Nephroma parile									0	0	0	2	0.01	0.01		
Nephroma resupinatum	0			2					0	0	0	1	+	0.01		
Parmelia hygrophila	4	0.33	0.44	5	2.13	0.69	−4.75	0.002	4	0.14	0.16	5	1.06	0.45	−4.75	0.002
Parmelia sulcata	5	6.38	3.32	5	3.01	1.00	2.18	0.077	5	0.75	0.41	5	0.86	0.65	−0.08	0.940
Parmeliopsis ambigua	5	0.34	0.21	5	0.06	0.07	3.30	0.014	5	0.96	0.62	5	1.67	1.27	−1.16	0.286
Parmeliopsis hyperopta	4	0.05	0.03	4	0.50	0.07	0.08	0.935	5	0.14	0.06	5	4.63	2.43	−6.73	0.002

	Branch epiphytes								Trunk epiphytes							
	Second growth			Old growth					Second growth			Old growth				
	f	$\bar{x}$	*s*	*f*	$\bar{x}$	*s*	*t*	*p*	*f*	$\bar{x}$	*s*	*f*	$\bar{x}$	*s*	*t*	*p*
Peltigera aphthosa									0			2				
Peltigera collina	0			1					0			1				
Peltigera membranacea									0			2				
Physcia stellaris	1			0					2			0				
Platismatia glauca	5	2.49	2.77	5	8.44	4.13	−3.05	0.016	2	0.10	0.19	5	8.39	6.56	−5.05	0.005
Pseudocyphellaria anomala	0			1												
Ramalina farinacea									1			0				
Ramalina pollinaria									1			0				
Ramalina thrausta	0	0	0	2	0.01	0.02			2	0.01	0.01	3	0.02	0.03	−0.86	0.415
Usnea lapponica	3	0.02	0.03	3	0.02	0.02	0.14	0.895	2	0.01	0.01	1	+	0.01	0.52	0.617
Usnea sp.	1			0												
Xanthoria polycarpa	1	+	0.01	0	0	0										
Mosses																
Antitrichia curtipendula	0	0	0	1	0.03	0.06			0			1				
Aulacomnium androgynum									1			0				
Brachythecium leibergii									4			4				
Brachythecium salebrosum									0	0	0	1	+	0.01		
Brachythecium starkii									1			0				
Campylium chrysophyllum									4			2				
Claopodium bolanderi									0			1				
Dicranum fuscesens									3			5				
Dicranum scoparium									1			2				
Dicranum tauricum									0	0	0	5	0.18	0.14		
Drepanocladus uncinatus	0			1					2			4				
Eurhynchium pulchellum									2			5				
Heterocladium procurrens									1			1				
Hypnum circinale									0			1				
Isopterygium seligeri									0			1				
Isothecium myosuroides	0			1												
Lescuraea stenophylla									2			0				
Mnium spinulosum									2			4				
Orthotrichum affine									0			1				
Orthotrichum speciosum	1	+	0.01	2	0.06	0.10	−1.16	0.300	0	0	0	2	0.02	0.03		
Plagiothecium laetum									1			2				
Pohlia nutans									1			0				
Pterigynandrum filiforme									0			1				
Rhytidiopsis robusta									2			3				
Tortula ruraliformis									1			0				
Liverworts																
Lepidozia reptans									1			1				
Lophozia ascendens									0			1				
Ptilidium pulcherrimum	0			2					0	0	0	5	0.54	0.40		

NOTE: Two-sample *t*-values and p (type I error) for the null hypothesis of no difference between second growth and old growth are given for species occurring in both stand age classes. Cover values were arcsine–square root transformed. Species with only frequencies listed were found in the whole-plot reconnaissance but were not in the microplots. The many bryophytes not encountered in the microplots on trunks resulted from excluding the tree bases from the microplots but including them in the whole-plot reconnaissance. +, value between 0 and 0.01.

TABLE 5. Frequency of occurrence (f = number of stands), mean percent cover ($\bar{x}$), and standard deviation of percent cover (s) for ground-layer bryophytes and lichens in five second-growth and five old-growth stands

	Second growth			Old growth				
	f	$\bar{x}$	s	f	$\bar{x}$	s	t	p
Lichens								
Alectoria imshaugii	1	0.03	0.08	1	0.07	0.15	−0.43	0.682
Alectoria sarmentosa	0	0	0	1	0.03	0.08		
Bryoria fuscescens	1			0				
Cetraria chlorophylla	1	0.03	0.08	2	0.07	0.09	−0.63	0.545
Cetraria orbata	0	0	0	1	0.03	0.08		
Cladonia bacillaris	1	0.03	0.08	0	0	0		
Cladonia carneola	2			0				
Cladonia cenotea	2	0.10	0.15	0	0	0		
Cladonia chlorophaea	4	0.30	0.22	3	0.17	0.17	1.10	0.305
Cladonia coniocraea	5	0.50	0	5	0.47	0.08		
Cladonia cornuta	1	0.03	0.08	0	0	0		
Cladonia fimbriata	5	0.50	0	5	0.43	0.09		
Cladonia multiformis	3	0.20	0.22	1	0.03	0.08	1.62	0.167
Cladonia ochrochlora	0	0	0	1	0.03	0.08		
Cladonia sulphurina	2			0				
Cladonia verruculosa	1			0				
Nephroma parile	0	0	0	3	0.20	0.22		
Nephroma resupinatum	0			2				
Parmeliopsis ambigua	5	0.30	0.14	4	0.20	0.14	1.15	0.283
Parmeliopsis hyperopta	5	0.27	0.09	4	0.27	0.22	−0.02	0.986
Peltigera aphthosa	1	0.03	0.08	3	0.20	0.22	−1.62	0.167
Peltigera membranacea	4	0.23	0.19	5	0.43	0.09	−2.10	0.082
Platismatia glauca	0	0	0	4	0.20	0.18		
Mosses								
Antritrichia curtipendula	0	0	0	1	0.03	0.08		
Atrichum selwynii	0	0	0	2	0.07	0.09		
Aulacomnium androgynum	5	0.37	0.14	5	0.47	0.08	−1.41	0.206
Brachythecium hylotapetum	5	0.93	0.81	5	0.63	0.40	0.75	0.485
Brachythecium leibergii	4	0.53	0.49	5	0.83	0.46	−1.00	0.345
Brachythecium salebrosum	5	0.50	0	5	0.73	0.81		
Brachythecium starkii	1	0.03	0.08	1	0.03	0.08	0	1.000
Bryum caespiticium	1			0				
Bryum sandbergii	0	0	0	2	0.07	0.09		
Buxbaumia piperi	0	0	0	1	0.03	0.08		
Campylium chrysophyllum	4	0.02	0.18	4	0.27	0.19	−0.55	0.601
Claopodium bolanderi	1	0.03	0.08	1	0.03	0.08	0	1.000
Dicranum fuscesens	3	0.20	0.22	4	0.30	0.18	−0.77	0.462
Dicranum polysetum	1	0.07	0.15	0	0	0		
Dicranum scoparium	4	0.23	0.19	4	0.47	0.52	−0.94	0.389
Dicranum tauricum	5	0.67	0.37	5	1.00	0.75	−0.90	0.406
Drepanocladus uncinatus	4	0.23	0.15	2	0.13	0.22	0.83	0.431
Eurhynchium pulchellum	0	0	0	5	0.97	0.78		
Eurhynchium praelongum	0	0	0	1	0.03	0.08		
Fissidens bryoides	0	0	0	2	0.07	0.09		
Heterocladium procurrens	0	0	0	5	0.24	0.15		
Hylocomium splendens	2	0.07	0.09	2	0.13	0.18	−0.70	0.508
Hypnum circinale	0	0	0	1	0.07	0.15		
Isopterygium seligeri	3	0.10	0.09	2	0.13	0.18	−0.33	0.753
Lescuraea stenophylla	1	0.03	0.08	0	0	0		
Mnium spinulosum	3	0.10	0.09	5	1.63	2.10	−1.63	0.178
Orthotrichum speciosum	0	0	0	1	0.03	0.08		
Plagiothecium laetum	2	0.07	0.09	1	0.03	0.08	0.63	0.545
Pleurozium schreberi	5	1.00	0.99	2	0.20	0.27	1.73	0.148
Pohlia nutans	4	0.37	0.22	1	0.03	0.08	3.22	0.024
Polytrichum juniperinum	5	0.40	0.15	2	0.10	0.15	3.20	0.013
Ptilium crista-castrensis	2	0.10	0.15	1	0.03	0.08	0.89	0.410
Rhytidiadelphus triquetrus	1	0.03	0.08	3	0.20	0.22	−1.62	0.167
Rhytidiopsis robusta	4	0.70	0.85	5	0.67	0.37	0.08	0.937
Tetraphis pellucida	1			1				
Timmia austriaca	0	0	0	2	0.10	0.15		
Tortula ruralis	0	0	0	1	0.03	0.08		

TABLE 5 *(concluded)*

	Second growth			Old growth				
	f	$\bar{x}$	s	f	$\bar{x}$	s	t	p
Liverworts								
Anastrophyllum hellerianum	0	0	0	2	0.20	0.27		
Barbilophozia lycopodioides	0			1				
Cephalozia lunulifolia	1	0.03	0.08	1	0.03	0.08	0	1.000
Jamesoniella autumnalis	0	0	0	4	0.37	0.22		
Lepidozia reptans	0	0	0	1	0.03	0.08		
Lophozia ascendens	0	0	0	1	0.07	0.15		
Lophozia incisa	0	0	0	1	0.03	0.08		
Lophozia longiflora	1	0.03	0.08	0	0	0		
Lophozia ventricosa	1	0.03	0.08	1	0.07	0.15	−0.43	0.682
Ptilidium pulcherrimum	5	0.37	0.14	5	0.43	0.15	−0.75	0.474
Tritomaria exsectiformis	0	0	0	1	0.03	0.08		

NOTE: Two-sample t-values and p (type I error) for the null hypothesis of no difference between second growth and old growth are given for species occurring in both stand age classes. Cover values were arcsine-square root transformed. Species with only frequencies listed were found with the whole-plot reconnaissance but were not encountered in the belt transects.

old growth than expected by chance alone ($p = 0.07$). Of the 11 species of the fruticose lichen genus *Cladonia* identified from the ground layer, 6 species occurred only in second growth, and 1 was found only in old growth (Table 5). Two species of moss, *Pohlia nutans* and *Polytrichum juniperinum*, had greater cover in second growth ($p < 0.03$, Table 5).

Discussion

Second-growth stands in our study averaged 70–75 years old, while the oldest trees in old-growth stands exceeded 300 years. Density of trees was greater in second growth, but canopy cover, mean height, and basal area were all lower. Within-stand structural heterogeneity, as measured by variation in tree height and diameter, was much greater in old growth. These structural differences are typical for old-growth vs. second-growth temperate forests (cf. Falinski *et al.* 1988). Although depth of litter and duff did not differ between the two groups of stands, the volume and size of snags and the volume of both sound and rotten down logs was greater in old growth. Greater amounts of water-holding woody debris and the deeper canopy of old growth generally result in higher humidity (Franklin *et al.* 1981). These differences suggest that old-growth forests provide an environment that is more heterogeneous, more humid, and with more coarse woody debris than do near rotation-age second-growth forests that regenerate after a clearcut and burn treatment.

Our old-growth stands fit standard definitions for old growth by having numerous large live trees, multispecies canopies, greater structural diversity, and well-developed multilayered canopies (Thomas 1979; Franklin *et al.* 1981; Old Growth Definition Task Group 1986). Although our old-growth stands had fewer and smaller snags than Pacific slope forests (Spies *et al.* 1988), they have more than the lower limit of 4 snags/ha used by the Old Growth Definition Task Group (1986) for mixed conifer stands on the Pacific slope and 1.2 snags/ha used by Thomas (1979) for the Blue Mountains of Oregon and Washington. Large amounts of down logs is also considered a characteristic attribute of old-growth forests (Old Growth Definition Task Group 1986).

Although combined cover of the pendant fruticose lichens *Alectoria* and *Bryoria* was comparable in the two groups of stands, different species dominated in each. Both *Alectoria sarmentosa* and *Alectoria imshaugii* were more abundant in the canopy and trunk strata of old-growth stands. Of the common species of *Bryoria*, *Bryoria capillaris* was more common in old growth, while *Bryoria fuscesens* and *Bryoria pseudofuscesens* were more abundant in second growth. *Alectoria* and *Bryoria* are important winter food for the endangered mountain caribou (Edwards *et al.* 1960; Rominger and Oldemeyer 1989; Servheen and Lyon 1989). In addition they provide nesting material for flying squirrels (Maser *et al.* 1985) and some species of birds.

In all three strata, nitrogen-fixing foliose lichens in the genera *Leptogium*, *Lobaria*, *Nephroma*, *Peltigera*, and *Pseudocyphellaria* were more common in old-growth stands. *Lobaria pulmonaria* had relatively high cover on branches and trunks of old growth and was lacking in second growth. In the canopies, *Nephroma helveticum* was found only in old growth. On trunks and in the ground layer, *Nephroma parile* and *Nephroma resupinatum* occurred only in old growth. Species of *Peltigera* were found in the trunk stratum only in old growth, and both *Peltigera aphthosa* and *Peltigera membranacea* were more abundant in the ground stratum in old growth. These results suggest that these relatively large, broad-lobed species thrive in the more equable climate found in old-growth stands. Nitrogen-fixing lichens are an important source of nitrogen in forests on the Pacific slope (Denison 1979, 1989; Pike 1978). These species are generally much less abundant in inland forests; however, they may still play a role in nitrogen cycling in these systems.

Old-growth forests provide better or more abundant habitat for most liverworts than do second growth forests in our area. Of 11 species of leafy liverworts, 7 were found only in old growth, while only 1 species occurred only in second growth. Two of the three most common species were found only in old growth. Many liverworts are obligate epixylics, requiring wood in later stages of decay to maintain viable populations (Söderstrom 1988). In addition many hepatics are drought-sensitive (Sharp 1939; McCullough 1948; Söderstrom 1988) and are able to survive better in the more humid microenvironments provided by old-growth forests.

Cladonia species were more numerous and abundant in second growth. Although some species occurred on down logs, many species were most common on stumps, a habitat much more abundant in second growth. Species of *Cladonia* were more abundant in second-growth coniferous forests in Sweden and are thought to be adapted to relatively high light and low humidity (Esseen 1983; Söderstrom 1988).

Major differences exist in lichen and bryophyte communities of canopy, trunk, and ground strata between managed second-growth forests and old-growth forests. The differences in our study area appear fairly consistent with those in other boreal and montane forests. For example, of six macrolichens reported as possible ''old forest'' lichen epiphytes in Scottish boreal forests (Rose 1976), three occur in our area and two of those were more abundant in our old growth than in second growth.

Environmental factors most likely controlling the distribution of bryophytes and lichens in these stands are light, humidity, climatic equableness, quantity and quality of coarse woody debris, and long-term continuity of the woody vegetation (Busby *et al.* 1978; Longton 1980; McCune and Antos 1981*a*, 1982; Söderstrom 1988). Many of these factors depend on stand structure, which is appreciably different between second-growth and old-growth forests. Furthermore, many species of brypohytes have limited dispersal capabilities (Söderstrom 1989). Consequently, in a highly fragmented landscape with only scattered source areas, they may be unable to colonize newly available habitat resulting from secondary succession. As more old-growth forest is converted to managed stands, lichens such as *Alectoria sarmentosa*, nitrogen-fixing species, and numerous species of liverworts will decline in abundance.

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